

Growth Changes in Internal and Craniofacial Flexion Measurements

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ABSTRACT Growth changes in both internal and craniofacial flexion angles are presented for *Pan troglodytes*, *Gorilla gorilla*, and modern humans. The internal flexion angle (IFA) was measured from lateral radiographs, and the craniofacial flexion angle (CFA) was calculated from coordinate data. Stage of dental development is used as a baseline for examination of growth changes and nonparametric correlations between flexion angles and dental development stage are tested for significance. In *Gorilla*, the IFA increases during growth. The IFA is relatively stable in *Pan* and modern humans. *Pan* and *Gorilla* display an increase in the CFA. However, this angle decreases during growth in modern humans. Flexion angles were derived from coordinate data collected for several early hominid crania. Measurements for two robust australopithecine crania indicate strong internal flexion. It has been suggested that cerebellar expansion in this group may relate to derived features of the posterior cranial base. In general, australopithecine crania exhibit craniofacial flexion intermediate between great apes and modern humans. The “archaic” *Homo sapiens* specimen from Kabwe is most similar to modern humans. *Am J Phys Anthropol* 110:47–56, 1999.

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A fundamental feature of the skull that displays considerable variation within and among hominoid species is the angulation (flexion) of the midline cranial base (Ross and Ravosa, 1993). The degree of flexion may be quantified using a number of different angles. Previous craniometric angles studied were reviewed by Moore (1981).

Internal flexion angles are often measured between the basicranial axis and its anterior extension. The basicranial axis extends approximately between basion and the region of the pituitary fossa, while its anterior extension is usually considered to extend from the pituitary fossa to a midline point of the upper face (e.g., nasion). Such angles are often referred to as the sphenoethmoidal angle (Dean, 1986).

Craniofacial flexion angles are defined by points that lie along the external surface of the basioccipital and palate. Thus, these angles measure the angulation between the facial skeleton and cranial base. Laitman et al. (1978) used the term exocranial flexion to refer to such angular measurements. More recently, Delson and Dean (1993) measured a “basal” angle between basion, sella, and the anterior hard palate to quantify the angulation of the face. Craniofacial flexion

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has been used as a feature in phylogenetic analysis of fossil hominoids (Ward and Brown, 1986).

Recent ontogenetic studies have improved our understanding of interspecific variation in hominoid craniofacial morphology (Bromage, 1992; McCollum, 1993; Kyauka, 1994). Although previous studies have described growth changes in certain flexion angles for extant hominoids (e.g., Ashton, 1957), growth changes in other critical flexion measurements remain poorly documented. In this paper, we test hypotheses related to growth changes in flexion angles for *Pan troglodytes*, *Gorilla gorilla*, and modern humans. Flexion angles for several early hominid crania are presented and interpreted in light of these ontogenetic data.

MATERIALS AND METHODS

The sample consists of ontogenetic series of *Pan troglodytes*, *Gorilla gorilla* and modern human crania that are part of the Hamann-Todd collection housed at the Cleveland Museum of Natural History. Additional young human crania housed at the Armed Forces Institute of Pathology are also included. Each cranium is assigned a dental age score (DENTAGE) which indicates the number of permanent maxillary molars in occlusion. DENTAGE is coded as follows: 0—all stages before occlusion of first permanent molars; 1—first permanent molars in occlusion; 2—second permanent molars in occlusion; 3—third permanent molars in occlusion. The stage of dental development has long been regarded as a useful baseline for the examination of craniofacial growth changes (Ashton, 1957; Scott, 1958; Laitman et al., 1978). Although relatively few dental stages are used here, this classification provides sufficient discrimination among juvenile crania to detect growth changes.

The internal flexion angle (IFA) is measured between the anterior end of the cribri-form plate (at the intersection with the internal contour of the frontal bone), tuberculum sellae, and basion and is approximately the angle between the floor of the anterior cranial fossa and the basicranial axis (Fig. 1a). This is a "true" internal flexion angle since the points used to define it are all located along the internal surface of the

cranial base. The IFA is measured from tracings of lateral radiographs using a digitizing tablet with Jandel Sigma Scan software. Crania to be radiographed were carefully positioned in the sagittal plane and only those with minimal duplication of bilateral structures (e.g., the dental arches) were selected for measurement.

The craniofacial angle (CFA) is measured between staphylion, hormion, and basion and is approximately the angle between the posterior edge of the vomer and the external surface of the basioccipital (Fig. 1b). According to Laitman et al. (1978), this angle measures the orientation of the basiocciput and indicates the positioning of the pharyngeal constrictor muscles. As noted above, however, one may also use this angle as a measurement of mid-facial positioning. The CFA was generated from coordinate data collected using a stereometric range of motion sensor (Sheffer et al., 1978). The coordinate data had been previously collected as part of the first author's dissertation study (May, 1998) which addresses both ontogenetic and interadult variation in craniofacial morphology. Craniofacial angles for eight of the juvenile modern human crania (housed at the Armed Forces Institute of Pathology) were collected from tracings of lateral radiographs. The two different methods for collection of flexion angles yield quite consistent results. Repeated measurements using coordinate-based and radiographic methods differed by less than 1°.

To investigate growth changes in flexion, correlations between flexion angles and stage of dental development (DENTAGE) are tested for significance. Because one of the variables is only ordinal in scale, a nonparametric correlation coefficient (Kendall's τ) is tested. Flexion angles are plotted against DENTAGE for each species. *T*-tests are used to test for sex differences in flexion angles among adults. Statistics are calculated using SPSS 8.0 for Windows.

Internal flexion measurements for fossil crania attributed to *Australopithecus africanus* (Sts 5), *A. boisei* (KNM WT 17400, CH1), *A. aethiopicus* (KNM WT 17000), and *Homo erectus* (KNM ER 3883) are derived from coordinate data collected from casts and original fossils housed at the Transvaal Mu-

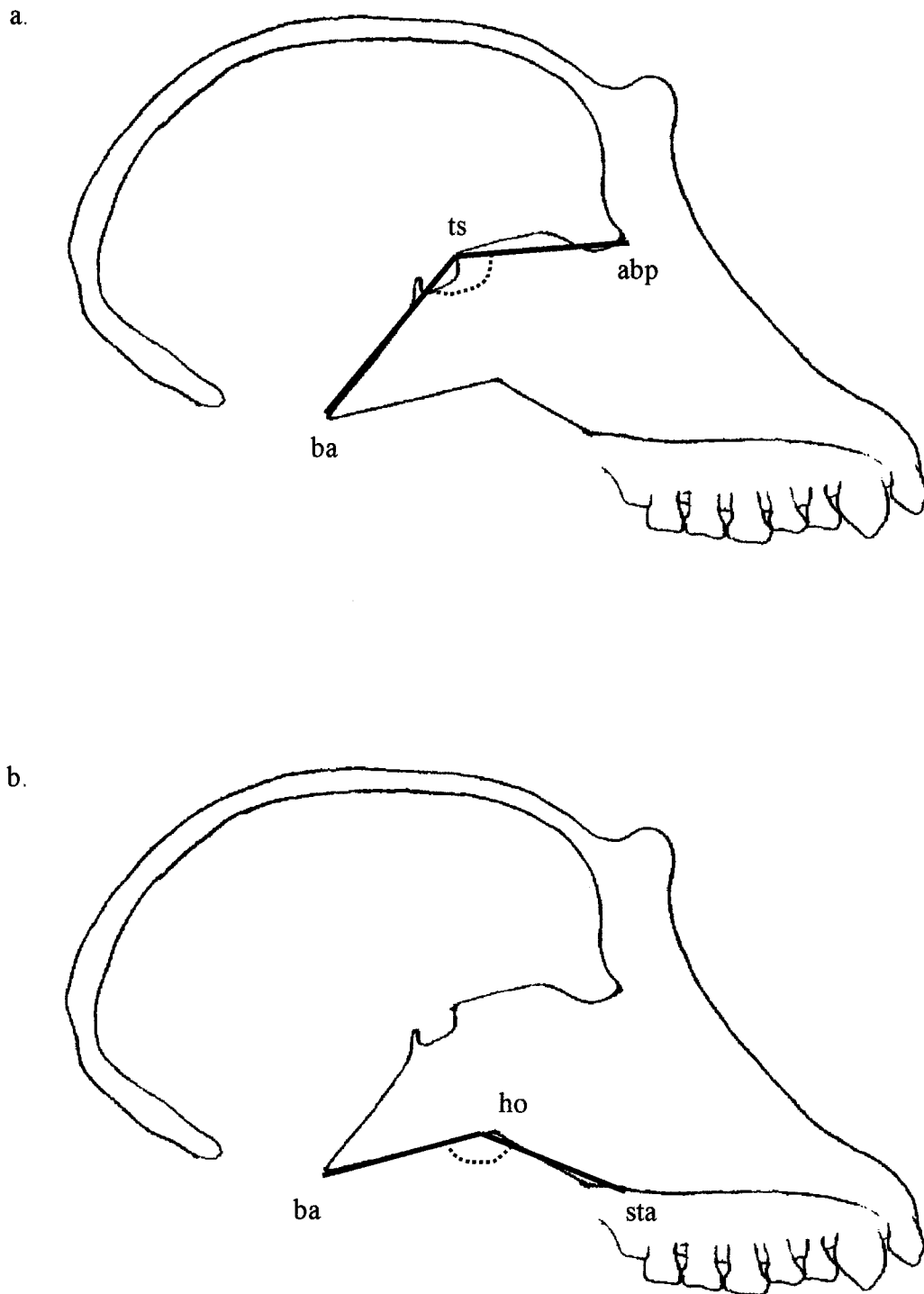


Fig. 1. Illustration of (a) landmarks used to define the internal flexion angle (IFA) and (b) landmarks used to define the craniofacial flexion angle (CFA).

seum and the Kenya National Museum. Coordinate data for fossil crania were collected using a Microscribe 3000 (Immersion Corporation) portable digitizer. The IFA for KNM WT 17400 is taken from a digitized cast of the internal cranial base. Since the clivus in the two *A. boisei* crania does not extend all the way to basion, the most inferior point on the endocranial surface of the clivus is used as an approximation of basion. Comparison of the region surrounding the clivus in these specimens with a cast of a complete *A. boisei* specimen (OH 5) suggests that only a small segment of the clivus is missing. Although the two *A. boisei* specimens are juveniles with maxillary M2s in occlusion, internal flexion changes after this stage are nonsignificant for extant taxa. Therefore, the IFAs measured from these specimens are compared to adult means for extant groups. The internal flexion angle for the *Homo erectus* specimen was obtained from an endocast of the original. Because the sphenoid body of KNM WT 17000 is damaged, the position of tuberculum sellae is estimated based upon the position of the optic canal.

Craniofacial angles are also derived from coordinate data collected from fossil crania attributed to *A. africanus* (Sts 5, MLD 37/38), *A. aethiopicus* (KNM WT 17000), *A. boisei* (KNM ER 406), and "archaic" *Homo sapiens* (Kabwe). Although the rear of the palate is damaged in KNM WT 17000, the preserved portion of the posterior edge of the palate extends nearly to the midline, and this most midline point was used to estimate the position of staphylion. These internal and craniofacial flexion measurements are compared to means for adult African apes and modern humans.

RESULTS

Table 1 lists summary statistics for internal and external flexion angles by DENTAGE and sex for *Pan*. Table 4 lists Kendall's τ coefficients for correlations between flexion angles and DENTAGE. In *Pan*, the IFA does not change significantly in the total or single-sex samples (Fig. 2a). The CFA increases significantly in the total and female-only samples (Fig. 3a and Table 2). Comparison of means for the total samples indicates that

TABLE 1. Mean and standard error of the mean for angular measurements (in degrees) in *Pan*¹

DENTAGE/ SEX	IFA		CFA	
	Mean	S.E.M. ²	Mean	S.E.M.
0 (U)	145.1 (5)	3.9	123.8 (4)	4.6
1 (T)	148.8 (12)	2.2	131.9 (11)	2.0
(M)	151.8 (1)	—	133.0 (1)	—
(F)	145.9 (5)	3.6	131.3 (5)	2.0
(U)	150.8 (6)	7.6	132.3 (5)	9.7
2 (T)	150.0 (14)	1.4	133.9 (10)	2.8
(M)	151.3 (4)	2.6	138.4 (4)	5.1
(F)	149.9 (7)	2.2	136.6 (3)	2.7
(U)	148.6 (3)	2.7	125.1 (3)	1.2
3 (T)	148.9 (46)	1.1	140.7 (36)	1.3
(M)	149.5 (16)	1.6	140.6 (11)	1.7
(F)	148.6 (30)	1.4	140.7 (25)	1.8

¹ IFA is the internal flexion angle; CFA is the craniofacial flexion angle. Sample sizes are in parentheses next to the mean values. (T = total sample, M = males, F = females, U = sex unknown.)

² Standard error of the mean.

the CFA increases from approximately 124° at the dm stage to 141° in adults. The greatest change appears to occur between stage dm and M1 and between M2 and M3 (Fig. 3a). *T*-tests for sex differences at the M3 stage are nonsignificant for both flexion angles.

Table 2 presents summary statistics for flexion angles in *Gorilla*. The IFA increases significantly in the total and male-only samples (Tables 2 and 4) indicating a progressive flattening of the internal cranial base. In the total samples, the IFA increases from approximately 149° to 157°. The CFA increases in *Gorilla* in the total sample only from approximately 132° to 139°. The CFA appears to be stable after the M2 stage in males and females (Fig. 3b). *T*-tests for sex differences are non-significant for both flexion angles.

In modern humans, the IFA displays a significant decrease in the total sample from approximately 135° to 130° (Fig. 2c and Table 4). Modern human crania are more flexed than *Pan* crania in the youngest dental development stage (Fig. 2a, c), suggesting that differences in internal flexion extend to the prenatal period. The CFA decreases in the total and male-only samples indicating an increase in the degree of external flexion. Human females have a significantly higher CFA than males.

Table 5 presents flexion angles for fossil hominid crania. Figure 4a compares IFA means for adult African apes and modern

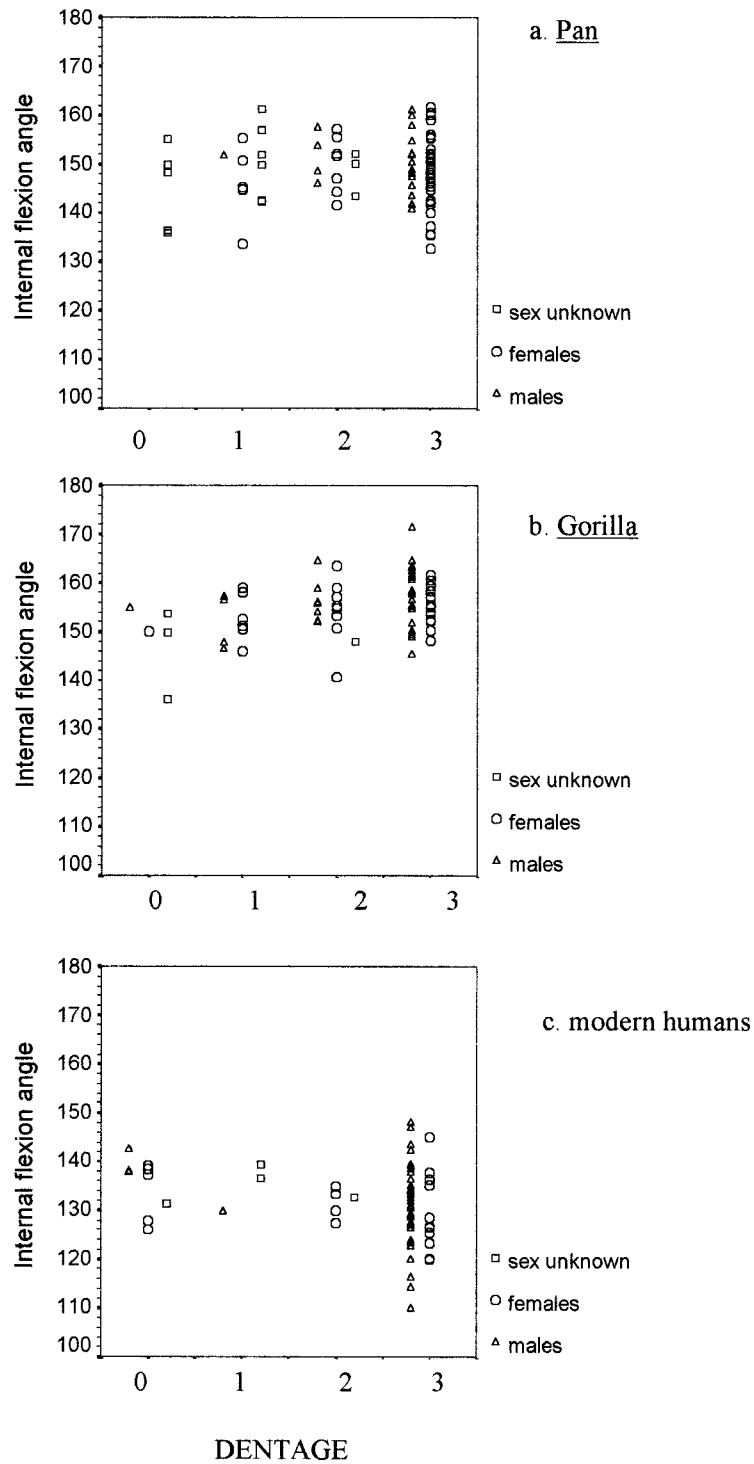


Fig. 2. The internal flexion angle (IFA) plotted against the dental age score (DENTAGE) for (a) *Pan*, (b) *Gorilla*, and (c) modern humans. Dentage is coded as follows: 0—all stages before occlusion of first permanent molars; 1—first permanent molars in occlusion; 2—second permanent molars in occlusion; 3—third permanent molars in occlusion.

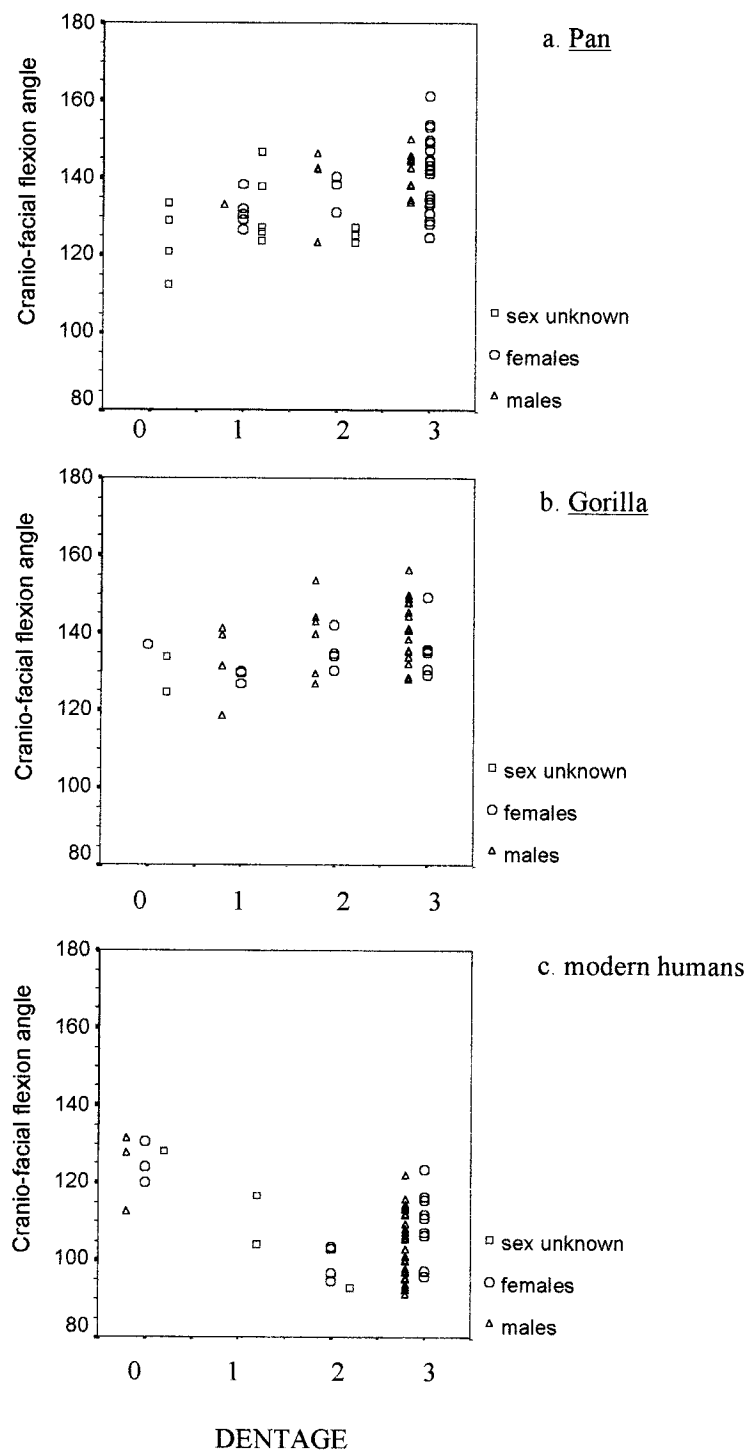


Fig. 3. The craniofacial flexion angle (CFA) plotted against the dental age score (DENTAGE) for (a) *Pan*, (b) *Gorilla*, and (c) modern humans.

TABLE 2. Summary statistics for angular measurements (in degrees) in *Gorilla*¹

DENTAGE/ SEX	IFA		CFA	
	Mean	S.E.M. ²	Mean	S.E.M.
0 (T)	149.1 (6)	2.8	131.7 (3)	3.6
(M)	154.9 (1)	—	—	—
(F)	150.0 (1)	—	136.8 (1)	—
(U)	147.4 (4)	3.9	129.2 (2)	4.5
1 (T)	152.5 (10)	1.6	130.8 (7)	2.9
(M)	151.9 (4)	2.8	132.3 (4)	5.1
(F)	152.9 (6)	2.0	128.8 (3)	1.0
2 (T)	154.7 (16)	1.4	137.2 (11)	2.3
(M)	156.2 (7)	1.7	139.0 (6)	4.0
(F)	154.3 (8)	2.4	135.1 (5)	1.9
(U)	147.9 (1)	—	—	—
3 (T)	157.0 (39)	0.8	139.3 (24)	1.6
(M)	157.9 (23)	1.3	140.4 (18)	1.8
(F)	155.6 (16)	0.9	135.9 (6)	2.9

¹ IFA is the internal flexion angle; CFA is the craniofacial flexion angle. Sample sizes are in parentheses next to the mean values. (T = total sample, M = males, F = females, U = sex unknown.)
² Standard error of the mean.

TABLE 3. Summary statistics for angular measurements (in degrees) in modern humans¹

DENTAGE/ SEX	IFA		CFA	
	Mean	S.E.M. ²	Mean	S.E.M.
0 (T)	135.4 (9)	1.9	124.2 (8)	2.3
(M)	139.4 (3)	1.5	123.6 (3)	5.8
(F)	133.8 (5)	2.8	123.6 (4)	2.5
(U)	131.4 (1)	—	128.0 (1)	—
1 (T)	135.3 (3)	2.9	110.3 (2)	6.3
(M)	129.8 (1)	—	—	—
(U)	138.0 (2)	1.4	110.3 (2)	6.3
2 (T)	131.7 (5)	1.3	98.1 (5)	2.2
(F)	131.4 (4)	1.7	99.4 (4)	2.3
(U)	132.6 (1)	—	93.0 (1)	—
3 (T)	130.7 (48)	1.2	105.5 (42)	1.4
(M)	131.0 (37)	1.4	103.9 (31)	1.6
(F)	129.5 (11)	2.4	109.9 (11)	2.4

¹ IFA is the internal flexion angle; CFA is the craniofacial flexion angle. Sample sizes are in parentheses next to the mean values. (T = total sample, M = males, F = females, U = sex unknown.)
² Standard error of the mean.

humans to that of several fossil hominid crania. Gorillas have the highest internal flexion angle, followed by chimpanzees and modern humans. The two specimens attributed to *A. boisei* are quite flexed internally. CH1 is within the modern human range while KNM WT 17400 is more flexed than any modern human in the sample. The IFA of KNM WT 17000 is closest to the mean for female *Gorilla*, while that of KNM ER 3883 is closest to that of *Pan*. The IFA of Sts 5 is between the means for *Pan* and modern humans.

Figure 4b compares adult values for the CFA. *Pan* and *Gorilla* are quite similar in

TABLE 4. Kendall's τ values for correlations between flexion angles and DENTAGE¹

	IFA	CFA
<i>Pan</i>		
(T)	.03 (77)	.41** (61)
(M)	-.14 (21)	.20 (16)
(F)	.04 (42)	.35** (33)
<i>Gorilla</i>		
(T)	.30** (71)	.29** (45)
(M)	.24* (35)	.19 (28)
(F)	.22 (31)	.28 (15)
Modern humans		
(T)	-.20* (65)	-.28** (57)
(M)	-.20 (41)	-.34* (34)
(F)	-.26 (20)	-.17 (19)

¹ IFA is the internal flexion angle; CFA is the craniofacial flexion angle. Sample sizes are in parentheses next to the coefficients.
 * $p < .05$, ** $p < .01$.

TABLE 5. Cranial base flexion angles (in degrees) for fossil hominid crania¹

	IFA	CFA
KNM WT 17000	153.2	125.7
KNM WT 17400	106.7	—
KNM ER 406	—	132.9
CH 1	124.1	—
Sts 5	141.0	133.9
MLD 37/38	—	126.7
KNM ER 3883	147.9	—
Kabwe	—	112.6

¹ IFA is the internal flexion angle; CFA is the craniofacial flexion angle.

the degree of external flexion while modern humans are flexed externally. CFAs for the four australopithecine crania (KNM ER 406, KNM WT 17000, Sts 5, and MLD 37/38) are above the range for modern humans and at the low end of the range for African apes. The CFA for the "archaic" *Homo sapiens* specimen from Kabwe is quite close to the mean for modern human females.

DISCUSSION AND CONCLUSIONS

Growth changes in internal flexion described in this study differ from those presented in previous studies. For example, our internal flexion angle was stable during postnatal development in *Pan*. Ashton (1957) found that a different form of the sphenoethmoidal angle increased to adult values of 159° in *Pan* and 169° in *Gorilla*. However, Ashton's sphenoethmoidal angle was defined using an anterior point located on the upper face and is not comparable to the IFA used in this study. In African apes, the upper face grows superiorly relative to points of

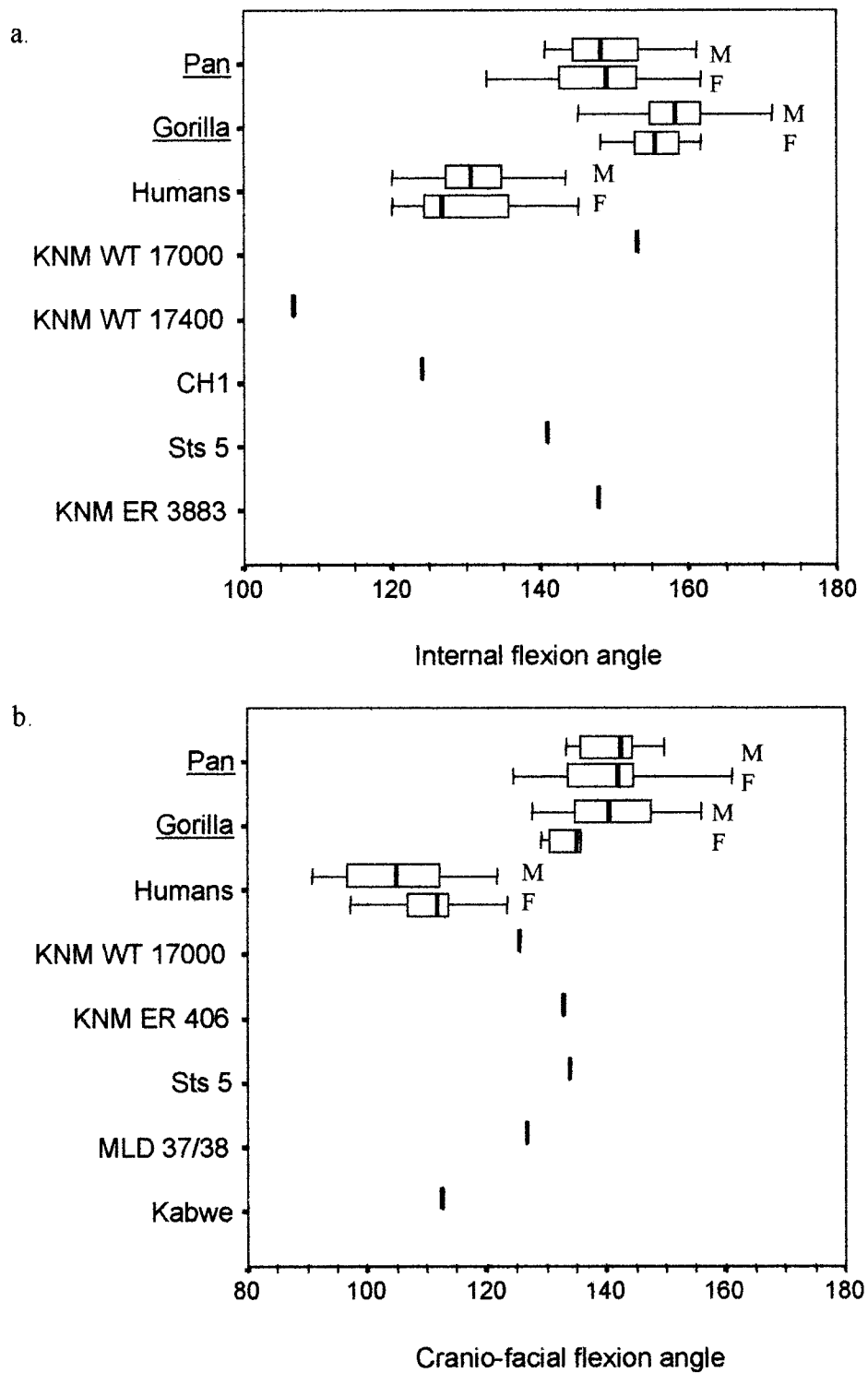


Fig. 4. Variation in the (a) internal flexion angle and (b) craniofacial flexion angle in adult samples of African ape and modern human crania and several fossil hominid crania. The vertical line in the box is the median and the limits of the box represent the 50% range. The whiskers indicate the maximum and minimum values.

the internal cranial base (Scott, 1963). Thus, sphenoethmoidal angles which employ upper face points will become progressively higher than the internal flexion angle used in this analysis and probably reflect both the pattern of facial growth and the internal deflection between anterior and posterior base segments. Scott (1958) measured the sphenoethmoidal angle between basion, prosphenion, and foramen cecum for a small growth series of *Pan* crania. Scott's angle is probably comparable to the internal flexion measurement used here and showed no consistent change across dental age categories.

In *Gorilla*, there is a progressive increase in the internal cranial base angle. This postnatal flexion change accounts for much of the difference in internal flexion between adult *Gorilla* and *Pan*. As discussed by Shea (1983), many of the shape differences between the two species probably relate to extension of an allometric growth pattern in *Gorilla*. Earlier studies have demonstrated that larger species or larger individuals within species tend to display less flexion of the cranial base (Biegert, 1963; Weidenreich, 1941).

In modern humans, the internal flexion angle decreases slightly during growth. Previous growth studies have also documented a progressive flexion of the modern human cranial base (George, 1978; Koski, 1961; Zuckerman, 1955). In a longitudinal study of flexion changes from 6 years to adulthood, Knott (1971) documented an decrease in the angle between pre- and post-sphenoidal cranial base segments. As in the present study, these angular changes were minor with an average decrease of less than 5°.

Growth changes in the craniofacial angle described here are consistent with those documented in previous studies. Laitman et al. (1978) found that external flexion decreased during growth in apes and increased during early postnatal life in modern humans. They related this ontogenetic change in flexion to growth of the upper respiratory system. Stark (1973) found a contrasting pattern of prenatal flexion change in *Pan* and *Homo*. During fetal growth, craniofacial flexion increased in *Homo* but not in *Pan*.

The robust australopithecine crania included in this study are highly flexed inter-

nally. Other robust australopithecine crania (e.g., OH5) seem to be internally flexed as well (Tobias, 1967; Walker and Leakey, 1988). It has been suggested that derived features of the posterior cranial base in robust australopithecines were related to encephalization (Dean, 1988). In later representatives of *A. boisei*, the cerebellum, posterior parietal and occipital portion of the cerebrum are expanded (Holloway, 1988).

The *A. africanus* specimen (Sts 5) is intermediate in the degree of internal flexion between *Pan* and modern humans. This result is in agreement with Ross and Henneberg's (1995) study in which Sts 5 and MLD 37/38 were found to be internally flexed. Our comparisons indicate that the *Homo erectus* specimen (KNM ER 3883) is remarkably unflexed internally. In fact, its IFA lies outside the range for modern humans. It is interesting to note that Ross and Henneberg (1995) measured internal flexion for a more recent hominid cranium attributed to "archaic" *Homo sapiens* (Kabwe) and found that it was also unflexed compared to modern humans.

In terms of craniofacial flexion, KNM ER 406, KNM WT 17000, Sts 5, and MLD 37/38 were found in this study to be within the range for African apes and outside the modern human range. Laitman and Heimbuch (1982) compared craniofacial flexion angles for nine early hominid crania to those of extant hominoids. The fossil crania were more similar to *Pan* and *Gorilla* than to modern humans. Our measurement for a more recent hominid cranium (Kabwe) indicated that this specimen was most similar to modern humans.

The results of this study suggest considerable independence between the form of the internal and external cranial base during growth. Ontogenetic changes in internal flexion are small compared to changes in external flexion. Pronounced internal flexion in robust australopithecine crania may relate to specialized enlargement of the cerebellum and posterior cerebrum, while variation in craniofacial flexion among early hominid crania may relate to differences in the facial growth pattern. An interesting question is whether phylogenetic change in craniofacial

flexion occurred at the same time as change in internal flexion.

Future studies should examine the relationship between internal and craniofacial flexion using more complete measurements of the complex contour of the cranial base. In addition, the influence of the growing brain on these angular relationships must be better understood.

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